

Table 3. Litter size and female weaning weight in litters produced by P and F₁ *Clethrionomys glareolus* females, weighed before breeding started

Mothers	Weight before breeding				Litter size				Weights of female young at weaning			
	N	\bar{x}	SD	Significance	N	\bar{x}	SD	Significance	N	\bar{x}	SD	Significance
P	40	18.5	2.1	P<0.001	141	4.9	1.2	P<0.05	219	9.1	1.9	NS
F ₁	35	16.0	1.9		85	4.5	1.4		77	10.0	1.5	

weight had appeared at maturity in the F₁ females from P litters. Thus a negative effect due to alternating large and small litters was supported also by the present data. It is obviously due to limited body resources (energy or nutrients) and the mobilizable amounts of these resources are probably related to body size.

The correlations in Table 2 are not significant. However, the interpretation of them as maternal effects on reproduction is supported both by similar findings in two American small rodent species and by significant differences in a derived relationship between litter sizes and female weights. Thus, although the reproductive effects are not as evident as the correlations in body weight both may be used for evaluating ideas relating to weight and reproduction in free-living populations.

One of the correlates of the proposed mechanisms in the Chitty Hypothesis for cyclic vole populations, i.e. a strong heritability of male body weights, was thus observed also in a non-cyclic vole population, thereby indicating a lack of importance of this factor in population dynamics. The negative maternal effect may be important in the demography of cyclic populations if the cyclicity is caused by other factors. In the present study it was observed under the same nutritional conditions for parents and offspring. However, the body growth improved in animals taken into the laboratory from the field and given surplus food (HANSSON 1985, unpubl.). In an increasing vole population there is more food per individual than in a peak population. Thus, the negative maternal effect should be much more obvious under field conditions in peak/decline populations. It may at least partly explain why increase-early peak animals reproduce early and have larger litters (HANSSON and HENTTONEN 1985b) and why late peak-decline animals show low body weight and late start of breeding, as evident for *C. glareolus* in, e.g., HANSSON (1984).

Summarizing, selective effects on individual characteristics related to body size do not cause vole cyclicity according to the Chitty Hypothesis while reproductive patterns in vole cycles, also appearing in the Chitty Hypothesis, may be explained by alternating positive and negative maternal effects.

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Zusammenfassung

Korrelationen von Wachstum und Reproduktion zwischen Eltern und Jungtieren bei der Rötelmaus Clethrionomys glareolus in Beziehung zur Chitty Hypothese

An nicht zyklischen Populationen von *Clethrionomys glareolus* wurden Korrelationen von Wachstum und Reproduktion zwischen Eltern und Jungtieren untersucht. Die Wechselbeziehungen in der Körpergröße waren positiv bei männlichen und negativ bei weiblichen Individuen. Die Wechselbeziehungen in bestimmten Fortpflanzungsparametern waren negativ und wurden weiter analysiert. Sie könnten durch einen negativen maternalen Effekt bedingt sein. Diese Befunde widersprechen der Chitty Hypothese zur Populationsregulierung, könnten aber die zyklischen Variationen von Gewicht und Reproduktion erklären, wenn äußere Faktoren die Zyklen beeinflussen.

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The swimming ability of *Ctenomys fulvus* (Ctenomyidae) and *Spalacopus cyanus* (Octodontidae), with reference to swimming in other subterranean mammals

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Abstract

Investigated the capacity for swimming for the South American rodents, *Ctenomys fulvus* and *Spalacopus cyanus*. Like most non-cricetid and non-murid rodent moles which have been tested, both *Ctenomys* and *Spalacopus* were not strong swimmers (mean swim time < two minutes). *Spalacopus* showed flexibility within a strong stroking pattern, but its shaggy pelage was detrimental to floating, which is of primary importance to the swimming success of all subterranean mammals tested thus far. As a result of small body size (small body mass to surface area ratio is conducive to floating since the dense pelage traps air which increases buoyancy), insectivore moles have for the most part performed better during swimming trials than rodent moles; it is interesting to note that no aquatic or semi-aquatic rodent-moles have evolved to parallel the swimming ability of certain species of talpids, despite rodent moles having much greater taxonomic diversity at the family, generic, and specific levels. Studies on the distribution and swimming ability of non-vagile subterranean mammals have thus far concerned the ability to disperse by swimming and climbing, the influence of water on burrow structure, geographic variation in behavioural patterns associated with the amount of free standing water, establishment of a more complete ethogram of the behavioural repertoire of subsurface animals, morphological factors influencing swimming ability, the evolution of fossoriality from an aquatic origin, and adaptive radiation into aquatic niches. Zoogeographic analysis of subterranean forms should consider swimming ability as an integral part of the factors responsible for current patterns of distribution.

Introduction

The swimming of tuco-tucos (*Ctenomys*, Ctenomyidae: Rodentia) and coruros (*Spalacopus*, Octodontidae: Rodentia) is of interest in several respects: firstly, ctenomyids are one of the few subterranean mammals which transport excavated soil with the hind feet (HICKMAN 1985), a behavioural trait which could have important implications as to the manner and ability of swimming; secondly, the swimming ability of South American small mammals is virtually unknown (disregarding domesticated species such as guinea pigs *Cavia porcellus*), as is the swimming ability of most small mammals (GETZ 1967; WILBER and WEIDENBACHER 1961; DAGG and WINDSOR 1972; ESHER et al. 1978; HARRIS and PETERSON 1979), so that chance or casual observations (FREDRICKSON 1972; STOCK 1972) are noteworthy as representing the only knowledge available for an entire genera or even families; finally, ctenomyids are the only major group of non-cricetid and non-murid subterranean eutherian mammals (see NEVO 1979 for an overview of subterranean mammal types) which have not been tested for swimming ability. With one of the last pieces of the puzzle in position, a number of trends should become apparent in the manner and ability of swimming; these general trends are discussed with comments on the significance of swimming ability to the biology of subterranean mammals as a group.

Materials and methods

One adult male (210 g) and adult female (314 g) *Ctenomys fulvus* were captured from San Pedro de Atacama, Region II, Chile, in September 1982. One subadult (65 g) *Spalacopus cyanus* was captured from Con Con Alto, Region V, Chile, in October 1982, and one adult male *S. cyanus* (190 g) was taken from Lagunillas, Region Metropolitana, Chile, in September 1982. Animals were air-freighted to South Africa where laboratory studies were undertaken.

Methodology followed the guidelines established for previous studies on the swimming ability of subterranean mammals (HICKMAN 1977, 1978, 1983; HICKMAN et al. 1983), permitting comparison with tests on swimming conducted under similar conditions.

Animals awaiting testing were housed separately in 31 cm wide, 92 cm long and 18 cm high all-glass terraria half-filled with sandy soil, at a temperature of 23°C. A 50 cm wide, 122 cm long and 43 cm high all-glass aquarium was filled to a height of 23 cm with water at 23°C. Animals were tested singly to obtain maximum performance (WILBER 1959, 1963; WILBER and HUNN 1960) between 8:00 h and 18:00 h, one trial per animal per day, three trials each, and the manner of swimming, speed, and endurance noted (documentation was by 35 mm photographs). Animals were removed from the water when it appeared as though the animals were in danger of drowning (about to sink without being able to resurface). Water was totally replaced for each trial to nullify any detergent effect urine might have on the air-trapping capacity of the pelage.

Following testing, animals were returned to their respective cages, where subsequent behaviour was noted.

Results

Ctenomys fulvus (mean 25.5 s) did not swim as well as *Spalacopus cyanus* (mean 85 s); no mortalities were incurred for either species.

Ctenomys fulvus

The 210 g male swam for 20, 15, and 30 s in progressive tests, while the 314 g female swam for 25, 20, and 55 s.

Twice during trials, the 210 g animal became totally immobile ("froze") when brought into contact with the water (a reaction to danger typical of many rodents), resulting in sinking without any effort to reach the surface. Even when stroking with the limbs occurred, splashing was never observed.

Swimming posture was horizontal (Fig. 1) with the eyes remaining open throughout the trials; however, the fur wetted rapidly, with the hindquarters gradually sinking until the tip of the snout was the last area to become submersed.

Propulsion by dog-paddle stroking did not involve sculling motions of the tail. The greatly enlarged hindfeet did not appear to hinder stroking, attaining maximum speeds of 30 cm/s. Turning involved little apparent effort.

Animals made no attempt at digging when returned to the cages after testing, but instead sat quietly on their haunches while grooming.

Spalacopus cyanus

The 65 g male swam for 45 and 165 s in progressive tests, while the 190 g male swam for 60, 25 and 25 s.

Stroking by *Spalacopus* commenced immediately upon contact with the water, without any splashing throughout the trials.

Body posture during swimming was at a slight angle to the surface (Fig. 2); nonetheless, the eyes positioned high on the head, normally useful when peering out of burrows, were kept well above the water while remaining open throughout the trials. The shaggy fur wetted quickly which required vigorous stroking for the animal to remain afloat.

The dog-paddle typical of many mammals was not supported by sculling of the tail (the short tail appeared highly tactile and was more useful as a probe rather than for



Fig. 1. Various views of *Ctenomys fulvus* swimming in an aquarium at 23 °C (drawn from photographs). *Above*: Side-view: note the horizontal body posture with snowshoe-like hindfeet; both fore and hindfeet with coordinated movements of the robust, tactile, tail (seen here partially lifted above the water) are also important in the transport of excavated soil. *Middle*: Three-quarter front view: the large foreclaws did not obstruct stroking, and the head with typically enlarged rodent incisors is maintained well above water level. *Below*: Top-view: only slight lateral movements of the hindquarters were noted; the tail was not used for sculling

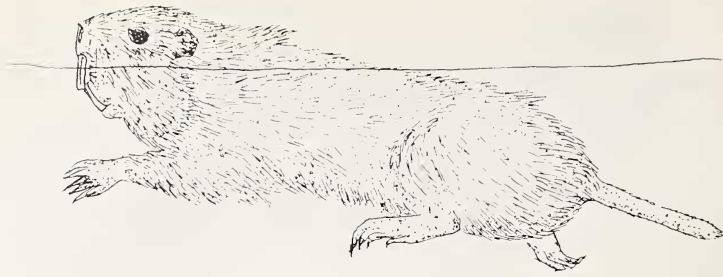


Fig. 2. Side view of *Spalacopus cyanus* during an aquarium trial at 23 °C (drawn from a photograph); note that the hindquarters remained low in the water, despite hindfeet positioning close to the body and strong stroking provided by all four limbs

propulsion); the dog-paddle switched to synchronous hindleg kicking when swimming rapidly in linear paths, although the forelimbs continued to stroke alternately. *Spalacopus* paddled strongly, so that it is surprising that the hindquarters remained low in the water during swimming. Swimming speed reached a maximum of 30 cm/s, with turns being executed with little apparent difficulty.

No attempts at digging were made by animals when returned to the cages; animals either rested quietly or groomed themselves.

Discussion

Adaptations of marine mammals to swimming has been well documented for some time (HOWELL 1930), while the swimming of most terrestrial mammals has remained almost totally unrecorded (DAGG and WINDSOR 1972). Except for some early observations on talpids (FISHER 1885; MERRIAM 1884; FOOT 1941; REED and RHINEY 1943), the swimming ability of all subterranean mammals was unknown until recently (see Table), despite the

Table. Classification of subterranean mammals tested for swimming ability, habitats sampled, projected width (m × min) of traversable water barriers, and sources of data

Order	Family	Genera tested	Capture site	Projected distance (m)	References
Insectivora	Talpidae	<i>Condylura</i>	Lake shore	1440	HICKMAN 1984b
		<i>Parascalops</i>	Lake shore	1080	
		<i>Scalopus</i>	Meadow	150	
	Chrysochloridae	<i>Amblysomus</i>	Grassland	360	HICKMAN 1986
		<i>Eremitalpa</i>	Desert	<1	
		<i>Chryso spalax</i>	Forest	8	
Rodentia	Geomyidae	<i>Thomomys</i>	Mountains	84	HICKMAN 1977
		<i>Geomys</i>	Plains	26	
		<i>Pappogeomys</i>	Plains	18	
	Bathyergidae	<i>Heterocephalus</i>	Semi-desert	54	HICKMAN 1983b
		<i>Cryptomys</i>	Grassland	35	
	Rhizomyidae	<i>Tachyoryctes</i>	Grass, few trees	40	HICKMAN 1983a
	Octodontidae	<i>Spalacopus</i>	Mountains	38	Present study
	Ctenomyidae	<i>Ctenomys</i>	Semi-desert	9	Present study
	Spalacidae	<i>Spalax</i>	Mountains, desert	1	HICKMAN et al. 1983

fact that moles and mole-rats are generally very poor climbers (HICKMAN 1982) and are thereby committed to swimming should water rise to sufficient levels. Flat areas, and highways (HUEY 1941), and rivers (KENNERLY 1963; SMITH and PATTON 1980) are moist areas which form corridors for dispersal, and are habitats particularly vulnerable to flooding. Normally non-vagile due to the high energy costs associated with excavating burrows (VLECK 1979), subterranean mammals may thus be induced to disperse from established areas and facilitate gene flow as animals "hurdle" edaphic barriers while swimming. Moreover, colonization is facilitated as re-establishment of burrows is not excessively difficult in moist and friable soils upon reaching the shoreline. The above scenario must however, meet one very important basic requirement: the animals must be able to swim. Rafting does not appear to be of much consequence, since subterranean mammals made no attempt at clinging to or climbing on buoyant debris provided during some of the testing.

The swimming ability of *Ctenomys fulvus*, representing one of the last major eutherian families of subterranean mammals to be tested (Table), reinforces the general pattern which has emerged from previous studies: insectivore moles are, as a general rule, better swimmers than rodent-moles (Fig. 3). For those species tested, the mean swimming time for insectivore moles was 20 min to only three minutes for rodent moles and swimming rate 21 m/min to 12 m/min in favour of insectivore moles, resulting in a projected (m × min) overall advantage in dispersal distance of 608 m to only 34 m to the advantage of insectivore moles. The above figures are likely minimal, as favourable currents and larger sample sizes over many years would undoubtedly reveal greater dispersal powers. None-

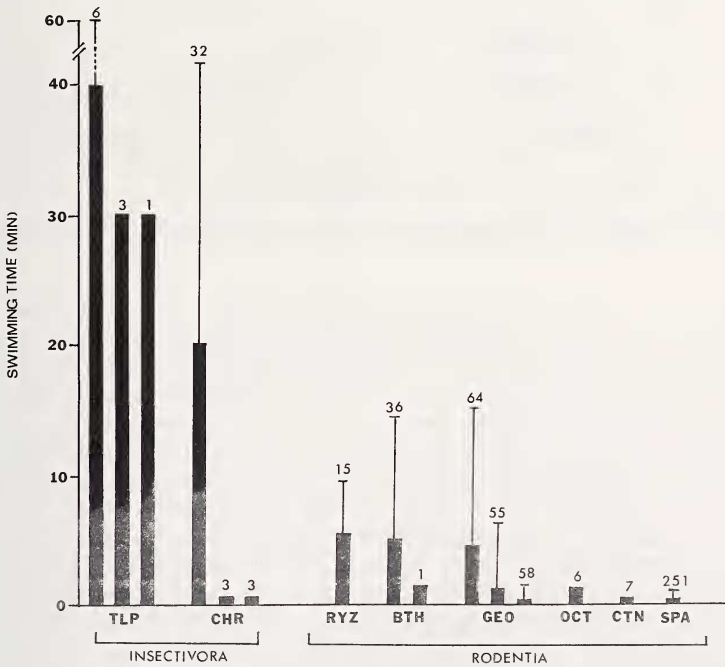


Fig. 3. Mean swimming times recorded for several species belonging to the major groups of eutherian subterranean mammals under laboratory conditions are indicated by bars; lines atop bars indicate the upper ranges during trials; the number of trials are given at the top of each line. TLP = Talpidae; CHR = Chrysochloridae; RYZ = Rhizomyidae; BTH = Bathyergidae; GEO = Geomyidae; OCT = Octodontidae; CTN = Ctenomyidae; SPA = Spalacidae. References for data and species for each column are listed in the Table

theless, laboratory testing has indicated an ability to traverse at least small waterways which may form an effective barrier to even surface rodents (SAVAGE 1973).

Insectivore vs Rodent moles

Size and pelage appear to be primarily responsible for the dichotomy in swimming performance between insectivore and rodent moles. The smaller size and weight of insectivore moles (a mean of 100 g to 146 g for rodent moles tested, see Fig. 4) results in a

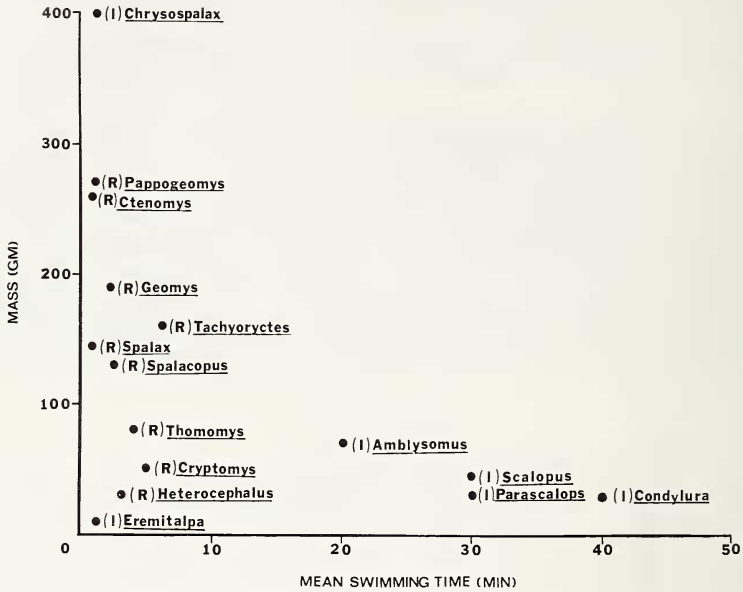


Fig. 4. Mean body mass of species plotted against mean swim times of insectivore (I) and rodent (R) moles

small body mass to surface ratio, with air trapped in the pelage exerting a greater influence on the buoyancy of swimming animals; the fur of talpids (the most successful subterranean mammal swimmers tested thus far) is renowned for thickness and insulative properties which not only assists floating, but protects talpids (which are small in size) from rapid temperature loss to the water. The uncharacteristic poor performance by an insectivore mole, the giant mole *Chrysothalpa*, was largely attributable to the inability of these large animals to float (HICKMAN 1986), while the smallest of the rodent-moles tested (*Heterocephalus*) did not perform well due to the lack of fur and subsequent lack of floating ability (HICKMAN 1983b). None of the rodent-moles were able to float effectively due to the large skull and massive head musculature important to digging and gnawing vegetation; insectivore moles do not dig with the head and have lighter skulls with only moderately developed jaw musculature for crushing insects and severing earthworms. Moreover, talpids have an elongate snorkle-like snout which enables the nostrils to be held high above the water surface (HICKMAN 1984b). Other non-subterranean rodent species such as the fossorial muskrat *Ondatra zibethica* are good swimmers despite a large size (WILBER 1958, 1963), so that factors other than size and pelage must also contribute to swimming success for mammals in general.

Anatomical features other than size and pelage appear of less importance to the swimming ability of subterranean mammals. Although insectivore moles (the best

swimmers) are more characteristically blind than rodent moles, the only rodent-mole with eyes completely covered with skin (*Spalax*) was one of the worst of all mammal swimmers; all subterranean mammals, whether effective swimmers or not, maintained equilibrium when swimming. The more prominent mystacial vibrissae of rodent moles, important to other species of rodents during swimming (AHL 1982), appeared only minimally to assist with balance. The "comb" fringing the lateral edge of the foot of *Ctenomys fulvus* did not play a significant role for propulsion or balance.

Although the best swimmers (the talpids) were tailed, the next best swimming group (the chrysochlorids) lack any form of external tail; and although the worst rodent-mole swimmer (*Spalax*) lacks an external tail, the best rodent-mole swimmers (*Cryptomys*) have only a short, stubby tail. The tail is of some assistance as a probe and for maintaining balance in some moletypes not only during digging (HICKMAN 1984c) but also during swimming (BEST and HART 1976; HICKMAN 1979); the tail was utilized for propulsion when swimming only by *Condylura*, and then only during diving (*Condylura* was the only species tested which attempted diving).

The development of enlarged foreclaws for digging had little effect on swimming (geomyids vs bathyergids, for example), but the partial webbing of the digits common to many subterranean mammals (responsible for the misnomer *Scalopus aquaticus*, a non-aquatic species), normally utilized when pushing soil, appeared to contribute to effective stroking in the water (HANAWALT 1922). Other preadaptations to swimming common to both insectivore and rodent moles include a streamlined body contour, strong nasal sphincters, ability to withstand low oxygen levels, and powerful limb musculature.

The fact that *Ctenomys* differs from most subterranean mammals by transporting excavated soil to the surface by kicking with the back legs rather than turning around and pushing the soil with the anterior portion of the body (HICKMAN 1985) had no discernable effect on either the manner or ability to swim. In fact, most behavioural differences had little influence on swimming ability. A few insectivore and rodent moles remained motionless and floated instead of trying to swim, so that the fur wetted less quickly due to less water turbulence; however, immobile animals would stand little chance of reaching the safety of the shore under natural conditions. *Spalax* was one species where a few individuals were able to improve on swimming performance by utilization of a characteristic "head lift" (HICKMAN et al. 1983).

Predicting swimming ability

With convergent anatomical adaptations and little behavioral differentiation in swimming behaviour, how predictable is a species performance in water? Two general trends emerge from studies on the swimming ability of subterranean mammals: 1. insectivore moles swim better than rodent-moles; 2. smaller species of mole types swim longer than larger mole types. There are, of course, exceptions to the trends; the large size of *Chrysoxalax* for an insectivore mole is the exception to the first trend which substantiates the second trend. Yet, one of the few species of any mammal mole-type to adapt to an aquatic existence, the talpid *Desmana* (250–400 g), has an adaptation of many aquatic mammals: large size (relatively speaking) for low surface to body mass ratio which conserves heat and offers some degree of protection from predatory amphibians (PINE 1975), fish, or birds. On the other hand, the Pyrenean desman (*Galemys*, 50–80 g) retains the small size of most subterranean mammals, as has an aquatic insectivore shrew, *Neomys* (10–20 g). Surprisingly, although talpids include the aquatic *Desmana* and semi-aquatic *Condylura*, the other insectivore mole-group, the chrysochlorids, have not radiated into even the semi-aquatic habit (HICKMAN 1986), and the only reference found for any group of rodent-mole was for the ctenomyid *Ctenomys lewisi* (WALKER 1975 p. 1047) which, "... tunnels in stream banks and may be semi-aquatic". There is little to suggest in the present study on *C. fulvus*

or any other rodent-mole that any species of rodent-mole regularly visits water and swims, despite the promise of plentiful food resources, a means of escaping predators, and extensive energy savings (VLECK 1979) by circumventing the need for excavating extensive tunnel systems. No mole-type has widely colonized the marine littoral environment (McCULLY 1967) although some species (*Bathyergus*) may be found in dunes. Since the subterranean environment is stable, reliable, and safe (most moles are K-selected), adaptive pressures would have to be very strong to promote abandonment of the sub-terrestrial niche and the risks involved with numerous novel situations.

Perhaps habitat differences between various mole types may give some indication of swimming ability. Subterranean mammals establish tunnel systems in a wide variety of habitats (Table), with insectivores more characteristically inhabiting moister areas where invertebrates are more numerous. Rodent-moles are also abundant in moist areas where there is an abundance of plants to eat, but are also found in drier areas less characteristic of insectivore moles where tubers, bulbs, and other geophytes are available. Insectivores from moist areas are much better swimmers, even swimming through water-filled tunnels (MOORE 1939). Rodent-moles (*Spalax*) from mountainous areas with seasonal flooding are better swimmers than con-specifics from desert habitat (HICKMAN et al. 1983). HICKMAN (1977) also suggests that regular spring-flooding in mountainous areas would select for swimming adaptations in geomyids (*Thomomys* were the best geomyid swimmers tested); however, BAINTER and HART (1979) cite good drainage in mountainous areas as not selecting for swimming ability. In any event, much water is seasonally available in mountainous areas, and a potential influence on swimming ability. Habitat may affect body size, amount of fat deposits, development of musculature, oiliness of the pelage, and many other physical characteristics which might indirectly affect buoyancy and swimming; however, no systematic studies have been conducted to determine the effect of these factors, and predicting swimming ability remains tenuous at best.

Moreover, there is a need for wider experimentation with a wider range of mammalian types before further generalities can be formulated and the significance of the results appreciated. In comparison with some rodent species (ESHER et al. 1978), insectivore moles compare quite favourably, yet other rodents such as *Microtus* swim at least as well as insectivorous moles (CARTER and MERRITT 1981; FISHER 1961), a characteristic which has enabled colonization of coastal islands.

The value of studies on swimming

Aside from practical value (evaluating flooding as a control measure for mole-types in agricultural or horticultural areas, as a test for the effectiveness of drugs (SHAPIRO et al. 1970), or as a water barrier for zoological gardens), there is heuristic value in having a comprehensive ethogram for mammals; many numerous and widely distributed animals (*Ctenomys*, for example, which extend almost the entire length of South America) have remained totally untested for swimming ability. Swimming ability, not as an end in itself but in conjunction with other factors, can be an important tool to zoogeographic analysis (SMITH and PATTON 1980; WILKINS 1985), enabling more knowledgeable interpretation of such behaviours such as position of the nest and direction of tunnel extension (MILLER 1957; WILLIAMS 1976). Thus far, studies on the swimming ability of subterranean mammals have involved the importance of various morphological, behavioural and abiotic factors (HICKMAN 1978, 1982, 1983b) to swimming success; phylogenetic affinities by use of behaviour as a taxonomic tool (HICKMAN 1977); the question of an aquatic vs terrestrial origin for talpids (HICKMAN 1984a); examination of the question why subterranean mammals have not more widely radiated into aquatic niches (HICKMAN 1986); the ecology of seasonal flooding (HICKMAN 1983a); and the importance of water as a barrier to dispersal and subsequent speciation (KENNERLY 1963; HICKMAN et al. 1983).

Concerning mammals as a group, areas of study such as the ontogeny of swimming ability remain largely unexplored (KING 1961; SCHAPIRO et al. 1970; DAGG and WINDSOR 1972), while further studies are needed to compare swimming performances within genera (SCHMIDLEY and PACKARD 1967; HAFNER and HAFNER 1975), within (EVANS et al. 1978) or between (HICKMAN and MACHINE 1987) families, and even between orders (STARRETT and FISHER 1970). Much further basic experimentation and understanding in terms of events which occur only rarely or remain for the most part unobserved is needed for a full appreciation and evaluation of free water as a significant feature in dispersal, adaptive radiation, and general biology of subterranean mammals, or indeed, of mammals in general.

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Zusammenfassung

Die Schwimmfähigkeit von Ctenomys fulvus (Ctenomyidae) und Spalacopus cyanus (Octodontidae) im Vergleich zu anderen subterranean Säugetieren

Die Schwimmfähigkeit von *Ctenomys fulvus* (Ctenomyidae) und *Spalacopus cyanus* (Octodontidae) wurde untersucht. Wie die meisten anderen bisher untersuchten, wühlenden Nager sind diese Arten mit durchschnittlich unter 2 min Schwimmzeit wenig ausdauernde Schwimmer. Hinderlich bei *Spalacopus* war offensichtlich sein schnell durchnässendes Fell.

Ein Vergleich der Schwimmfähigkeit bei wühlenden Nagern und Insektenfressern ergab: Wühlende Insektenfresser (untersucht wurden Talpidae und Chrysochloridae) sind im Durchschnitt bessere Schwimmer als wühlende Nager. Innerhalb der Gruppen wühlender Nager hat sich keine Art an das Wasserleben angepaßt, wie das die Desmaninae innerhalb der Talpidae getan haben.

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